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The relationship between fish condition and the probability of being mature in American plaice (*Hippoglossoides platessoides*)

M. Joanne Morgan

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Fish condition can be related to a population's reproductive potential in a variety of ways. The relationship between condition and the probability of being mature (adult) was examined in three populations of American plaice (*Hippoglossoides platessoides*). The effect of condition was tested after first removing the known effects of age and length. Neither relative liver condition nor relative body condition significantly affected the probability of male American plaice being mature, but there was a significant positive effect of both condition indices on the probability of being a mature female. However, the additional variation explained by female condition was small when compared with the combined effect of age and length. Condition is related to the age and size at which fish attain adulthood. Variation in fish condition will have a direct impact on the spawning stock biomass of a population through differences in the maturation schedule of cohorts with differing condition.

Keywords: body condition, liver condition, maturation, reproductive potential.

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M. J. Morgan: Department of Fisheries and Oceans, PO Box 5667, St John's, Newfoundland A1C 5X1, Canada; tel: +1 709 772 2261; fax: +1 709 772 4105; e-mail:morganj@dfo-mpo.gc.ca.

Introduction

Measures of fish condition based on weight at a given length and liver size relative to body size are thought to be reliable indicators of the energetic condition or energy reserves of fish (Lambert and Dutil, 1997). Poor condition is usually associated with poor feeding and/or environmental conditions, and fish in poor condition may suffer increased natural mortality (Dutil and Lambert, 2000). In adult fish, condition can have dramatic effects on reproductive potential. The egg production of fish in poor condition may decrease through lower potential fecundity, atresia, or even skipped spawning (Burton and Idler, 1987; Kjesbu *et al.*, 1991; Marshall *et al.*, 1998; Rideout *et al.*, 2000), and the larvae produced by fish in poor condition may be smaller and less likely to survive (Marteinsdottir and Steinarsson, 1998). All these factors may lead to a relationship between fish condition and recruitment (Marshall and Frank, 1999). A further potential impact of poor condition of spawning fish is that they may be at greater risk of mortality following spawning (Lambert and Dutil, 2000).

The probability of a fish being mature (i.e. adult) increases with size and age (Korsbrekke, 1999; Morgan and Colbourne, 1999). There may be an additional relationship with condition so that fish in better condition are more likely to be mature. Few studies have examined this effect. Marteinsdottir and Begg (2002) found an increased proportion of mature fish at a given size or age for those cod (*Gadus morhua*) that were in better condition. Bromley *et al.* (2000) found that a low food ration in adolescent turbot (*Scophthalmus maximus*) could lead to failure to mature. Some studies have also revealed a positive impact of fish weight on the probability of being mature (Ajiad *et al.*, 1999; Cook *et al.*, 1999; Bromley, 2003). If condition is related to the probability of being mature then this would be a further impact on a population's reproductive potential, through a direct effect on spawning stock biomass.

American plaice (*Hippoglossoides platessoides*) are widely distributed throughout the north Atlantic, and have displayed large changes in age and size at maturity since the 1960s. Morgan and Colbourne (1999) showed that the probability of being mature was inversely related to population size, and to some extent positively related to temperature and juvenile growth rate. Their study did not examine the relationship between condition and maturity, so the purpose of the current study was to determine whether such a relationship exists.

Material and methods

Data from male and female American plaice from three populations off Newfoundland, Canada, were examined: Labrador

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and northeast Newfoundland, for which data were available from Northwest Atlantic Fisheries Organization (NAFO) divisions 2J and 3K; the Grand Bank population, NAFO divisions 3L, 3N, and 3O; and St Pierre Bank in NAFO subdivision 3Ps (Figure 1). Data were available from 1993 to 2001 (2000 for 2J3K) from stratified random research vessel surveys conducted by the Canadian Department of Fisheries and Oceans. Surveys were conducted in autumn in 2J3K (mainly October–December) and in spring in 3LNO (mainly May–June) and 3Ps (mainly April).

All weights were measured at sea, using electronic balances. Total body weight and length were recorded for all fish sampled, and liver weight for a subsample of fish with body length ≥ 30 cm. Because the body weight of small fish is highly variable, only fish > 12 cm long were used in the analyses. Total body and liver weights were available for $> 28\,000$ and > 4000 fish, respectively (Table 1). Fish age was determined from otoliths. Fish were classed as adult (mature) or juvenile (immature) on the basis of macroscopic examination of their gonads, using the maturity classification of Templeman *et al.* (1978). Although this classification was developed originally for haddock (*Melanogrammus aeglefinus*), it has since been applied to most groundfish species off Newfoundland. The earliest stage is juvenile (immature), and all other stages show some evidence of maturing to spawn, spawning, or having spawned in the past, so for this study were classed as adults. American plaice are determinate batch spawners (Zamarro, 1992; Nagler *et al.*, 1999), so the classification is appropriate. However, because the species spawns mainly in spring (Pitt, 1966; Morgan, 2001), the times of sampling of the different populations relative to the time of spawning in this study are variable. This problem may be most acute for fish sampled in division 2J3K, i.e. in autumn. However, because the oocytes of American plaice begin maturing well in advance of the spawning season, opaque eggs are clearly visible by the time an autumn survey is conducted. For the 2J3K population, as spawning would not take place until the following year, 1 year was added to the age of the fish at the time of the survey.

Indices of condition were used to examine the effect of both liver and body weight. For body weight, the commonly used index of Fulton's K ($K = W/L^3$, where W is total body weight and L is length) showed an increasing trend with body length, so an alternative index, relative K (K_r) was used:

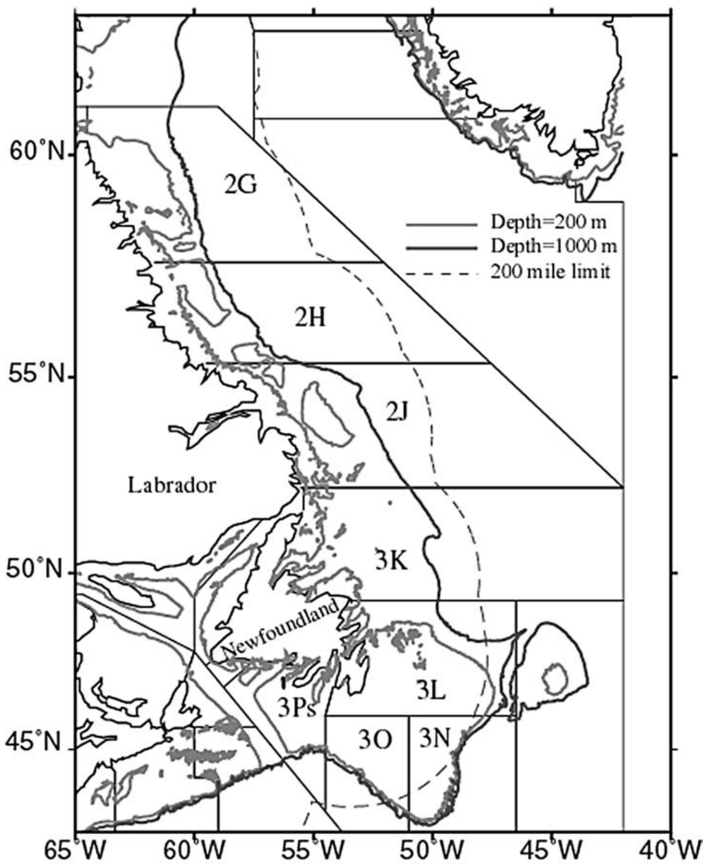

Figure 1. Map showing the study area. Data for the three populations of American plaice came from Labrador and northeast Newfoundland (divisions 2J and 3K), the Grand Bank population (divisions 3L, 3N, and 3O), and the St Pierre Bank (subdivision 3Ps).

Table 1. Sample sizes of American plaice available for each population, sex, and year for determining body and liver weight.

	Male			Female		
Year	2J3K	3LNO	3Ps	2J3K	3LNO	3Ps
Body weight						
1993	259	855	215	353	1115	335
1994	250	688	224	376	1027	327
1995	155	662	215	256	980	307
1996	220	917	304	322	1293	417
1997	256	883	330	389	1103	412
1998	302	829	355	480	1175	507
1999	229	908	353	421	1339	459
2000	180	930	381	315	1249	494
2001		759	330		1048	454
1993–2001	1851	7431	2707	2912	10 329	3712
Liver weight						
1993	20	138	39	99	176	64
1994	28	124	50	80	201	88
1995	7	72	39	46	142	70
1996	1	74	21	59	142	52
1997	6	88	30	36	162	57
1998	5	77	49	57	184	78
1999	0	99	48	54	213	71
2000	0	119	54	49	207	79
2001		117	48		208	82
1993–2001	67	908	378	480	1635	641

$$K_r = W/\widehat{W} \quad (1)$$

where $\widehat{W}$ is the predicted body weight from a length/weight relationship. The form of the length/weight relationship was $\log(W) = \text{intercept} + \log(L)$. Separate regressions were carried out for each combination of sex and population (2J3K, 3LNO, 3Ps), for a total of six regressions. In each case the regressions used data for all years combined. Examination of residuals from the length/weight relationships plotted against log of length indicated some obvious outliers, which were therefore removed (14 observations in total) and the regressions were refitted. To calculate K_r for an individual fish, its body weight was divided by the body weight predicted by the length/weight regression for a fish of that length, sex, and population. Use of this type of condition index removes the problems associated with systematic change in the index across length. However, the indices produced are comparable within a population and sex, though not between populations or between sexes.

Several indices were examined for liver weight: LW/W_G, where LW is liver weight and W_G is gutted body weight; LW/W; and $LK_r = LW/\widehat{LW}$ where $\widehat{LW}$ is the predicted liver weight from a length/liver weight relationship. Results of all three were similar, so LK_r was chosen because it has the same form as K_r. As for K_r, LK_r was calculated using log length/log liver weight relationships on data for all years combined, but calculated separately for males and females in each population. Outliers (37 observations) were removed as described above, and the log length/log liver weight regressions were refitted before the calculation of LK_r.

To determine whether the effect of LK_r or K_r on the probability of being mature was significant, generalized linear models (McCullagh and Nelder, 1983) were applied. In these models, fish were classed as either mature (1) or juvenile (0). All models had a logit link function and a binomial error structure. All parameters were modelled as continuous variables. As age and length affect the probability of being mature in this species (Morgan and Colbourne, 1999), the significance of LK_r or K_r was tested by determining whether there was a significant decrease in the deviance with the addition of the index to a model already containing age and length effects.

The proportion of the deviance accounted for by LK_r and K_r was also calculated. This value is the pseudo coefficient of determination, or pseudo r^2 (Swartzman *et al.*, 1992). The pseudo r^2 for these factors was calculated as the deviance in the model containing the intercept, age, and length effects minus the deviance once LK_r or K_r had been added to the model, divided by the null deviance of the model containing only an intercept. This provides a measure of the importance of LK_r and K_r relative to that of age and length.

Results

For male American plaice, LK_r ranged from 0.5 to 3 in 2J3K, from 0.3 to 2.4 in 3LNO, and from 0.3 to 2.7 in 3Ps.

However, there was no significant effect of LK_r on the probability of being mature for any of the populations once the effect of age and length had been accounted for. For females, LK_r ranged from 0.3 to 2.9 in 2J3K and 3LNO, and from 0.4 to 3.4 in 3Ps. There was a significant positive effect of liver condition on the probability of being mature for females in 3LNO ($\chi^2 = 36.3$, d.f. $= 1$, $p < 0.0001$) and 3Ps ($\chi^2 = 13.8$, d.f. $= 1$, $p < 0.0005$), and to a lesser extent for females in 2J3K ($\chi^2 = 4.6$, d.f. $= 1$, $p < 0.05$; Table 2, Figures 2 and 3). In all three cases, the additional proportion of the deviance accounted for by LK_r was small, just 0.02. On average, age and length together accounted for 20 times the deviance accounted for by LK_r (Table 2).

Although only a small portion of the deviance was accounted for by LK_r, there was a clear increase in the estimated probability of being mature with increasing LK_r. This is illustrated in Figure 2, in which the proportion mature is calculated by applying the parameter estimates from the model to a standard fish of age 8 years and length 33 cm, using the range of condition indices observed for that age and length in each population. For 2J3K plaice, the estimated proportion mature ranged from 0.8 to 0.9, for 3LNO from 0.3 to 0.7, and for 3Ps from 0.2 to 0.6. When the proportion mature was estimated at age for a smaller range of LK_r (0.8−1.2), there was a small increase in the proportion mature with increasing LK_r (Figure 3). The differences between populations shown in Figures 2 and 3 are the result of differing effects of age and size on maturation, as well as varying relationships with condition.

K_r for males ranged from 0.4 to 3 in 2J3K, from 0.3 to 2.6 in 3LNO, and from 0.5 to 2.3 in 3Ps. There was no significant additional effect of K_r on the probability of being mature for males in any of the populations after accounting for the effects of age and length. There was a significant additional positive effect of K_r on the probability of being mature for females in 2J3K ($\chi^2 = 45.7$, d.f. $= 1$, $p < 0.0001$), in 3LNO ($\chi^2 = 113.2$, d.f. $= 1$, $p < 0.0001$), and in 3Ps ($\chi^2 = 86.0$, d.f. $= 1$, $p < 0.0001$; Table 2, Figures 2 and 4). The range in K_r for females was 0.4−2.2 in 2J3K, 0.4−2.6 in 3LNO, and 0.5−2.4 in 3Ps. As was the case for LK_r, the proportion of the deviance accounted for by K_r was small: 0.01 in 2J3K, 0.006 in 3LNO, and 0.02 in 3Ps. On average, age and length together accounted for more than 60 times the deviance accounted for by K_r (Table 2).

Despite the small amount of deviance accounted for, there was a clear increase in the estimated proportion mature over the observed range of K_r for a fish of age 8 years and length 33 cm (Figure 2). For 2J3K, the range in the estimated proportion mature across the range of K_r was 0.8−1, for 3LNO 0.2−0.7, and for 3Ps 0.06−0.4. Greater K_r resulted in a larger estimated proportion mature at age for all stocks (Figure 4). The effect of condition (the difference between curves for a population at different levels of condition) appeared to be greatest for 3Ps, and smallest for 3LNO. Again, differences between populations in the estimates of proportion mature at age are the result of differences in the effects of age and size on the proportion mature, as well as the effect of condition.

Table 2. Results of generalized linear models testing for effects of relative liver condition index (LK_r) and relative body condition index (K_r) on the probability of being mature in female American plaice. The tests are conducted sequentially so that the significance of length is tested after accounting for the effect of age, and the significance of condition index is tested after the effects of age and length have been removed.

Stock	Effect	Deviance	χ^2	p	r^2
2J3K	Age	272.2	30.6	<0.0001	0.10
	Length	233.0	39.2	<0.0001	0.13
	LK_r	228.4	4.6	<0.05	0.02
3LNO	Age	931.3	630.9	<0.0001	0.40
	Length	821.0	110.2	<0.0001	0.07
	LK_r	784.7	36.3	<0.0001	0.02
3Ps	Age	393.0	274.5	<0.0001	0.41
	Length	347.4	45.6	<0.0001	0.07
	LK_r	333.6	13.8	<0.0005	0.02
2J3K	Age	2075.8	1993.0	<0.0001	0.49
	Length	1490.6	585.1	<0.0001	0.14
	K_r	1444.9	45.7	<0.0001	0.01
3LNO	Age	6282.2	8165.8	<0.0001	0.57
	Length	5196.2	1086.0	<0.0001	0.08
	K_r	5083.0	113.2	<0.0001	0.008
3Ps	Age	2029.7	3093.8	<0.0001	0.60
	Length	1710.7	319.0	<0.0001	0.06
	K_r	1624.7	86.0	<0.0001	0.02

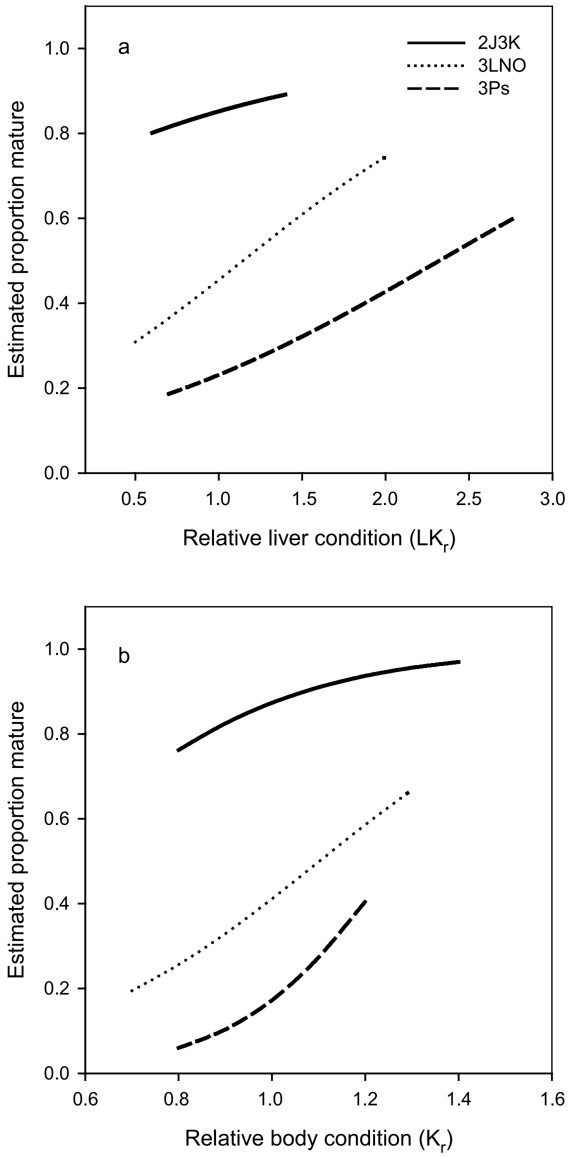

Figure 2. Estimated proportion of females mature at age 8 years and length 33 cm calculated from the fitted model for each population of American plaice. The proportion mature is calculated across the observed range of (a) relative liver condition, and (b) relative body condition in each population for a female age 8 and 33 cm long.

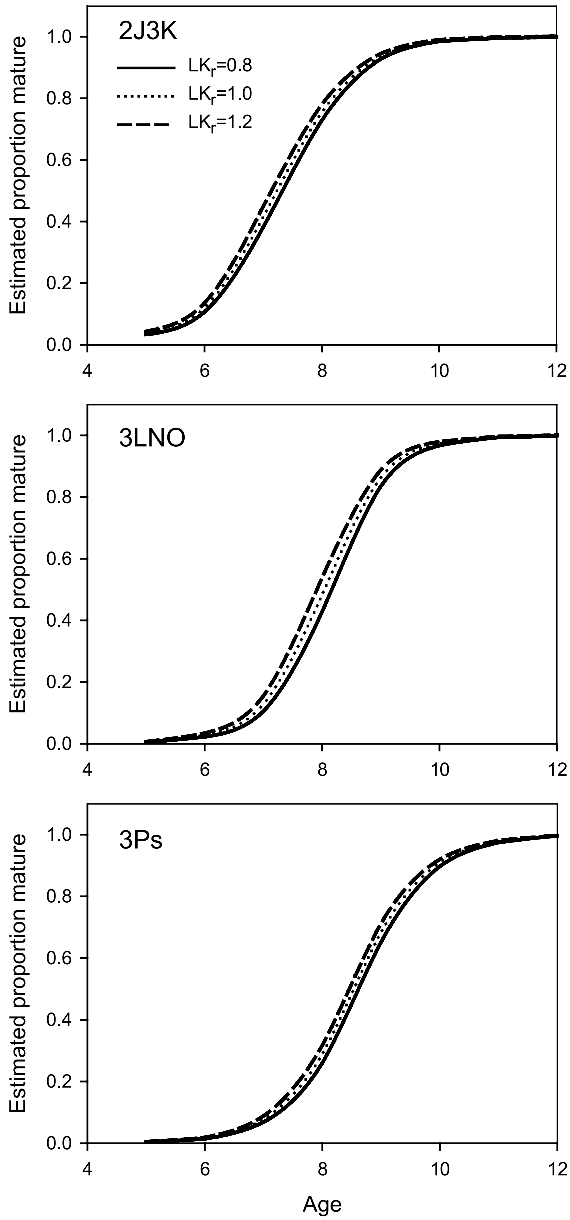

Figure 3. Estimated proportion of female American plaice mature at age from each of the three sampled populations at three levels of relative liver condition.

Discussion

Female American plaice were more likely to be mature if they were in better condition. This effect was in addition to the positive effects of age and size and was the case if measured by liver or body condition. Energy allocation involves trade-offs between growth and reproduction (Calow, 1985): fish in better condition may have more surplus energy to devote to reproduction and be able to make the "decision" to mature at a smaller size and younger age. Some previous studies have shown a positive effect of condition or weight on the probability of being mature (Ajiad *et al.*, 1999; Cook *et al.*, 1999; Bromley *et al.*, 2000; Marteinsdottir and Begg, 2002; Bromley, 2003). As fish condition often varies over time, the variability can have a direct impact on spawning stock biomass through differences in the maturation schedule of cohorts with differing condition.

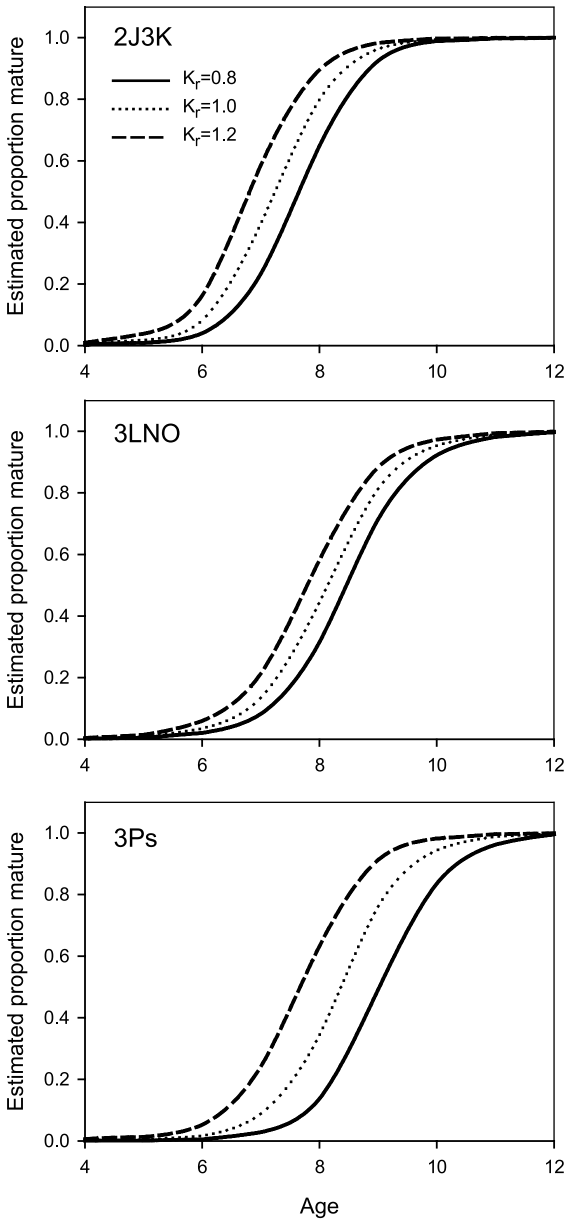

Figure 4. Estimated proportion of female American plaice mature at age from each of the three sampled populations at three different levels of relative body condition.

Many fish store energy in their liver, so indices of liver condition should be good indicators of overall fish condition (Lambert and Dutil, 1997). In addition, reserves stored in the liver seem to be used to produce vitellogenin, so it is not surprising that there is a relationship between liver condition and maturity (Norberg and Kjesbu, 1991). The significance of LK_r on the probability of being mature in this study was revealed despite the limited sample size and that liver weights were only determined for fish ≥ 30 cm long. At 30 cm, many female American plaice are already mature (Morgan and Colbourne, 1999). Therefore, the absence of fish <30 cm from the sample may have made the effect of liver condition more difficult to detect, and resulted in underestimation of its impact. There may be a better relationship between liver condition and maturity for smaller fish. Also, the truncated size distribution means that the function was fit across only the upper portion of the maturity curve; again this may result in underestimation of the magnitude of the effect of liver condition. The data set for K_r was much larger and spanned most of the size range of American plaice. Further, flatfish store much of their energy in their body tissue and are not as reliant as some fish on storage in the liver (Dawson and Grimm, 1980; Maddock and Burton, 1994), meaning that, in this case, K_r may be a better indicator of the effects of condition.

Male American plaice did not show a significant additional effect of condition on the probability of being mature. This is not surprising for the LK_r data because they are for fish ≥ 30 cm only, and most male American plaice are mature by that size (Morgan and Colbourne, 1999). However, there was also no significant effect of body condition. Male and female flatfish often mature at very different size and age, males maturing smaller and younger (Rijnsdorp and Ibelings, 1989; Morgan and Colbourne, 1999). Moreover, there can be differences in energy allocation between adults of the two sexes (Rijnsdorp and Ibelings, 1989; Bromley *et al.*, 2000). Differences in sex-specific energy allocation may be responsible for the differences in the effect of condition on maturation seen here.

The combined effect of age and length accounted for a much larger portion of the deviance than either LK_r or K_r. Although they analysed the effects of age and length separately, this is similar to the results found by Marteinsdottir and Begg (2002) for cod. The current difference in age at 50% maturity was small for a range of LK_r of 0.8−1.2. For K_r the difference in age at 50% maturity was greater, as much as 1.5 years for 3Ps. This result indicates that, although the relationship between condition and maturation was minor compared with that between maturation and age/length, it can have a substantial impact on maturation, potentially leading to very different numbers of spawners produced per recruit for fish maturing at different levels of condition.

There seemed to be some difference between populations in the extent of the effect of K_r on the proportion mature. The effect seemed greatest for 3Ps, and less for 2J3K and 3LNO. At this stage it is not possible to determine what may be causing this apparent interpopulation difference. However, the fish were sampled at different times relative to the spawning season. Condition in fish such as American plaice is known to vary seasonally, and its effect may be easier to detect at certain times of the year than at others (MacKinnon, 1972; Lambert and Dutil, 1997). The three populations also differ in age and size at maturity (Morgan and Colbourne, 1999), perhaps impacting the relationship between condition and maturity and/or the ability to detect it.

The reproductive potential of a population is affected by a variety of factors. Condition is directly related to the number and quality of eggs produced by a female (Burton and Idler, 1987; Kjesbu *et al.*, 1991; Marteinsdottir and Steinarsson, 1998; Rideout *et al.*, 2000). The results of this study show that fish condition is also related to the age and size at which fish attain maturity.

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References

Ajiad, A., Jakobsen, T., and Nakken, O. 1999. Sexual difference in maturation of northeast Arctic cod. Journal of Northwest Atlantic Fishery Science, 25: 1–15.

Bromley, P. J. 2003. The use of market sampling to generate maturity ogives and to investigate growth, sexual dimorphism and reproductive strategy in central and south-western North Sea sole (*Solea solea* L.). ICES Journal of Marine Science, 60: 52–65.

Bromley, P. J., Ravier, C., and Witthames, P. R. 2000. The influence of feeding regime on sexual maturation, fecundity and atresia in first-time spawning turbot. Journal of Fish Biology, 56: 264–278.

Burton, M. P., and Idler, D. R. 1987. An experimental investigation of the non-reproductive, post-mature state in winter flounder. Journal of Fish Biology, 30: 643–650.

Calow, P. 1985. Adaptive aspects of energy allocation. *In* Fish Energetics: New Perspectives, pp. 13–31. Ed. by P. Tytler, and P. Calow. The Johns Hopkins University Press, Baltimore, Maryland.

Cook, R. M., Kunzlik, P. A., Hislop, J. R. G., and Poulding, D. 1999. Models of growth and maturity for North Sea cod. Journal of Northwest Atlantic Fishery Science, 25: 90–99.

Dawson, A. S., and Grimm, A. S. 1980. Quantitative seasonal changes in the protein, lipid and energy content of the carcass, ovaries and liver of adult plaice, *Pleuronectes platessa* L. Journal of Fish Biology, 16: 493–504.

Dutil, J-D., and Lambert, Y. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 57: 826–836.

Kjesbu, O. S., Klungsoyr, J., Kryvi, H., Witthames, P. R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Canadian Journal of Fisheries and Aquatic Sciences, 48: 2333–2343.

Korsbrekke, K. 1999. Variations in maturity of haddock in the Barents Sea in relation to year-class strength, age, size, sex and area. Journal of Northwest Atlantic Fishery Science, 25: 37–45.

Lambert, Y., and Dutil, J-D. 1997. Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? Canadian Journal of Fisheries and Aquatic Sciences, 54(Suppl. 1): 104–112.

Lambert, Y., and Dutil, J-D. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Canadian Journal of Fisheries and Aquatic Sciences, 57: 815–825.

MacKinnon, J. C. 1972. Summer storage of energy and its use for winter metabolism and gonad maturation in American plaice (*Hippoglossoides platessoides*). Journal of the Fisheries Research Board of Canada, 29: 1749–1759.

Maddock, D. M., and Burton, M. P. M. 1994. Some effects of starvation on the lipid and skeletal muscle layers of the winter flounder, *Pleuronectes americanus*. Canadian Journal of Zoology, 72: 1672–1679.

Marshall, C. T., and Frank, K. T. 1999. The effect of interannual variation in growth and condition on haddock recruitment. Canadian Journal of Fisheries and Aquatic Sciences, 56: 347–355.

Marshall, C. T., Kjesbu, O. S., Yaragina, N. A., Solemdal, P., and Ulltang, O. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of northeast Arctic cod? Canadian Journal of Fisheries and Aquatic Sciences, 55: 1766–1783.

Marteinsdottir, G., and Begg, G. A. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. Marine Ecology Progress Series, 235: 235–256.

Marteinsdottir, G., and Steinarsson, A. 1998. Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. Journal of Fish Biology, 52: 1241–1258.

McCullagh, P., and Nelder, J. A. 1983. Generalized Linear Models. Chapman and Hall, London. 261 pp.

Morgan, M. J. 2001. Time and location of spawning of American plaice in NAFO Divisions 3LNO. Journal of Northwest Atlantic Fishery Science, 29: 41–49.

Morgan, M. J., and Colbourne, E. B. 1999. Variation in maturity-at-age and size in three populations of American plaice. ICES Journal of Marine Science, 56: 673–688.

Nagler, J. J., Adams, B. A., and Cyr, D. G. 1999. Egg production, fertility, and hatch success of American plaice held in captivity. Transactions of the American Fisheries Society, 128: 727–736.

Norberg, B., and Kjesbu, O. S. 1991. Reproduction in coldwater marine fish: applications in aquaculture. *In* Reproductive Physiology of Fish, pp. 239–243. Ed. by A. P. Scott, D. E. Sumpter, D. E. Kime, and M. S. Rolfe. FishSymp 91, Sheffield.

Pitt, T. K. 1966. Sexual maturity and spawning of the American plaice, *Hippoglossoides platessoides* (Fabricius), from the Newfoundland and Grand Bank areas. Journal of the Fisheries Research Board of Canada, 23: 651–672.

Rideout, R. M., Burton, M. P. M., and Rose, G. A. 2000. Observations on mass atresia and skipped spawning in northern Atlantic cod, from Smith Sound, Newfoundland. Journal of Fish Biology, 57: 1429–1440.

Rijnsdorp, A. D., and Ibelings, B. 1989. Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, *Pleuronectes platessa* L. Journal of Fish Biology, 35: 401–415.

Swartzman, G., Huang, C., and Kaluzny, S. 1992. Spatial analysis of Bering Sea groundfish survey data using generalized additive models. Canadian Journal of Fisheries and Aquatic Sciences, 49: 1366–1378.

Templeman, W., Hodder, V. M., and Wells, R. 1978. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of the southern Grand Bank. ICNAF Research Bulletin, 13: 53–65.

Zamarro, J. 1992. Determination of fecundity in American plaice (*Hippoglossoides platessoides*) and its variation from 1987 to 1989 on the tail of the Grand Bank. Netherlands Journal of Sea Research, 29: 205–209.